

Landmark research in legumes

R.J. Singh, G.H. Chung, and R.L. Nelson

Abstract: Legumes are members of the family Fabaceae or Leguminosae and include economically important grain legumes, oilseed crops, forage crops, shrubs, and tropical or subtropical trees. Legumes are a rich source of quality protein for humans and animals. They also enrich the soil by producing their own nitrogen in symbiosis with nitrogen-fixing bacteria. International centers and national institutes collect, maintain, distribute, and produce high-yielding legumes (grain-pulses, oilseeds, forages, nutraceuticals, medicinal shrubs, and trees). Legume breeders are confined within the primary gene pools (GP-1) in their varietal improvement programs and have not exploited secondary gene pools (GP-2), tertiary gene pools (GP-3), or quaternary gene pools (GP-4). Legumes are also an excellent source of timber, medicine, nutraceuticals, tannins, gums, insecticides, resins, varnish, paints, dyes, and eco-friendly by-products such as soy diesel. Three forage crops, *Medicago truncatula*, *Lotus japonicus*, and *Trifolium pratense*, are model legumes for phylogenetic studies and genome sequencing. This paper concludes that a "protein revolution" is needed to meet the protein demands of the world.

Key words: Fabaceae, grain legumes, soybean, groundnut, pulse crops, forage legumes, protein revolution, gene pools, genome sequencing.

Résumé : Les légumineuses font partie des Fabaceae ou de Leguminosae, deux familles qui comprennent des espèces importantes au plan économique dont des légumineuses à graines, des oléagineuses, des plantes fourragères, des arbustes ainsi que des arbres tropicaux ou subtropicaux. Les légumineuses constituent une riche source de protéines de qualité pour les humains et les animaux. Ils enrichissent également le sol en produisant leur propre azote en symbiose avec des bactéries fixatrices d'azote. Des centres nationaux et internationaux effectuent la collecte, le maintien, la distribution et le développement de légumineuses à haut rendement (légumineuses à graines, oléagineuses, fourragères, nutraceutiques, arbustes médicinaux et arbres). Les sélectionneurs de légumineuses sont confinés au sein des pools géniques primaires (GP-1) dans leurs efforts d'amélioration génétique et n'ont pas exploité les pools secondaires (GP-2), tertiaires (GP-3) ou quaternaires (GP-4). Les légumineuses constituent également une excellente source de bois, médicaments, nutraceutiques, tannins, gommes, insecticides, résines, vernis, peintures, colorants et sous-produits écologiques tels que le biodiesel d'huile de soya. Trois légumineuses fourragères (*Medicago truncatula*, *Lotus japonicus* et *Trifolium pratense*) sont des espèces modèles pour les études phylogénétiques et en séquençage génomique. Cet article conclut qu'une « révolution protéique » est nécessaire afin de rencontrer les besoins en protéines dans le monde.

Mots-clés : Fabaceae, légumineuses à graines, soya, arachide, légumineuses, légumineuses fourragères, révolution protéique, pools géniques, séquençage génomique.

[Traduit par la Rédaction]

Introduction

Legumes, members of the family Fabaceae or Leguminosae (also known as the pea and bean family), are the third largest flowering plant family following orchids (Orchidaceae) and daisies (Asteraceae or Compositae). This family includes 727 genera and 19 325 species (Lewis et al. 2005).

Legumes grow in wide agro-ecological conditions, and the plant morphologies vary from herbs to giant forest trees. Taxonomists have divided the Fabaceae into 3 major subfamilies based on morphological features, particularly flower traits. The 3 subfamilies have unequal distributions. The subfamilies have been traditionally classified as the Papilionoideae (476 genera and about 14 000 species), the Caesalpi-

Received 13 February 2007. Accepted 7 May 2007. Published on the NRC Research Press Web site at genome.nrc.ca on 5 July 2007.

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noioideae (162 genera and about 3 000 species), and the Mimosoideae (77 genera and approximately 3 000 species) (Doyle and Luckow 2003). The majority of species of Papilionoideae are herbaceous, though some are trees and shrubs. By contrast, the majority of species of Caesalpinioideae are tropical or subtropical trees and shrubs, while the Mimosoideae includes trees and shrubs; trees from the important genus *Acacia* are used for timber (International Legume Database and Information Service 2007).

Legumes include major grain legumes, oilseed crops, forage crops, ornamental crops, medicinal crops, and agroforestry species (Lewis et al. 2005). Major dietary grain legumes are common bean (*Phaseolus vulgaris* L.), cowpea (*Vigna unguiculata* (L.) Walp.), pigeonpea (*Cajanus cajan* (L.) Millsp.), chickpea (*Cicer arietinum* L.), faba bean (*Vicia faba* L.), lentil (*Lens culinaris* Medik.), mungbean (*Vigna radiata* (L.) Wilczek), azuki bean (*Vigna angularis* (Willd.) Ohwi & Ohashi), and pea (*Pisum sativum* L.). Grain legumes are valuable sources of protein for both humans and animals. Soybean (*Glycine max* (L.) Merr.) and groundnut or peanut (*Arachis hypogea* L.) are the major sources of vegetable oil. Forage legumes include alfalfa (*Medicago sativa* L.), clover (*Trifolium pratense* L.), and birdsfoot trefoil (*Lotus corniculatus* L.). Lupin (*Lupinus* species) is grown for multiple uses and the seed is rich in protein and oil and is used for animal feed. Legume vegetation is used for fodder, cover crop, and green manure. Other economically important legumes are guar (clusterbean) (*Cyamopsis tetragonoloba* L.), fenugreek (*Trigonella foenum-graecum* L.), grass pea (*Lathyrus sativus* L.), cicer milkvetch (*Astragalus cicer* L.), crownvetch (*Coronilla varia* L.), licorice (*Glycyrrhiza glabra* L.), lablab (*Lablab purpureus* (L.)), horsegram (*Macrotyloma uniflorum* (Lam.) Verdc.), winged bean (*Psophocarpus tetragonolobus* (L.) DC.), and tamarind (*Tamarindus indica* L.).

Legumes and cereals have co-evolved since ancient times. The characteristic feature of legumes is the presence of root and (or) stem nodules that contain nitrogen-fixing bacteria. Legumes have wide geographical distribution, constitute extensive morphological, physiological, and chemical diversity, and are an integral part of human civilization. They form complementary components of agricultural systems worldwide. Complementary pairings of legumes and grasses in regional diets include common bean and maize in South America; lentil, pea, chickpea, faba bean, and bitter vetch with 2 types of wheat (durum and einkorn), barley, and oat in the Middle East; soybean with rice in Eastern Asia; and cowpea with pearl millet and sorghum in Africa.

The Leguminosae are second only to the Gramineae in agricultural importance. Grain legumes alone contribute 33% of the dietary protein needs of humans (Graham and Vance 2003). While cereals are an excellent source of energy in the form of carbohydrates, legumes are the major source of dietary protein for a large proportion of humanity. Soybean, ground nuts, and grain legumes contain heart-healthy and antioxidant nutrients. Moderate consumption of legumes may help to prevent cardiovascular disease, stroke, Parkinson's, Alzheimer's, and Huntington's diseases, liver ailments, and even cancer (Singh 2005, 2007). Legumes are economically important in world trade because they are used for human food, animal feed, and other commercial applica-

tions (pharmaceutical products, soap, paints, resins, coatings, linoleum, cosmetics, lubrication, chemicals, plastic coatings, and ethanol).

Several legumes are considered model crops for genetic and molecular studies. The foundation for the science of genetics was accomplished by Johann Gregor Mendel based on his hybridization experiments in pea (see Singh 2005). Major milestones of recent international collaborations include genome sequencing of *Medicago truncatula* Gaertner, *Lotus japonicus* (Regel) K. Larsen, *Trifolium pratense*, and *Glycine max* using a combination of cytological, genetic, and molecular technologies (Sato et al. 2005).

The objective of this paper is to summarize landmark research in legumes including grain legumes, oilseed crops, and forage crops.

Establishment of international and national programs

The establishment of international and national research and germplasm centers was an important step toward improving major legumes of dietary importance. Each center concentrates on plant exploration, maintenance, distribution, and varietal improvement programs for specific legumes. These centers are as follows:

1. Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia (<http://www.ciat.cgiar.org>): Common bean is a mandate crop.
2. International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India (<http://www.icrisat.org>): Pigeonpea and chickpea are mandate crops.
3. International Center for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria (<http://www.icarda.org>): Chickpea, lentil, and faba bean are mandate crops. The center also maintains pea germplasm but has no active varietal improvement program.
4. International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria (<http://www.iita.org>): Cowpea is a mandate crop.
5. Asian Vegetable Research and Development Center (AVRDC), Shanhua, Tainan, Taiwan (<http://www.avrdc.org>): Vegetable crops, mungbean, and an edible vegetable soybean known as *edamame* (fresh green soybeans) are mandate crops of the institute. The center has the largest germplasm collection of mungbean and maintains azuki bean.
6. International Soybean Program (INTSOY), University of Illinois, Urbana-Champaign, Illinois, USA (<http://web.aces.uiuc.edu/intsoy/index.html>): INTSOY does not have a soybean varietal improvement program but promotes soybean products worldwide and is an international resource.
7. National programs: National (public) and private industries worldwide have legume improvement programs. The US Department of Agriculture (USDA) collects, maintains, and distributes germplasm of legumes. Large private companies such as Monsanto (<http://www.monsanto.com>), Pioneer (<http://www.pioneer.com>), and Syngenta (<http://www.syngenta.com>) and many smaller companies have legume varietal improvement programs. Major research efforts are being undertaken by national

institutions to sequence the entire genomes of model forage (*M. truncatula*, *L. japonicus*, and *T. pratense*) and oilseed (*G. max*) legumes.

Gene pools of legumes

Based on a review of literature on hybridization, Harlan and de Wet (1971) proposed a 3 gene pool concept—primary, secondary, and tertiary gene pools—for utilization of germplasm resources for crop improvement. Genetic resources have been developed using integrated, multidisciplinary approaches involving plant exploration, taxonomy, genetics, cytogenetics, plant breeding, microbiology, plant pathology, entomology, agronomy, physiology, distant hybridization, and molecular biology including cell and tissue culture, DNA analysis, and genetic transformation. These efforts have produced high-yielding legumes without anti-nutritional chemicals. The concept of gene pools for legumes is incompletely defined because breeders have confined breeding efforts to the primary gene pool and cytogenetic studies have been minimal. Secondary and tertiary or quaternary gene pools are based on phylogenetic relationships (Singh 2005).

Primary gene pool

The primary gene pool (GP-1) of legumes includes cultivated races, land races, biological species and subspecies, and weedy relatives. Crossing within this gene pool is easy, and the vigorous hybrids exhibit normal meiotic chromosome pairing and are fertile. Gene segregation in the F_1 is normal and gene exchange is generally easy. Primary gene pool A includes cultivated races and land races. Primary gene pool B includes subspecies and wild and weedy relatives. *Glycine soja* Sieb. & Zucc., a wild annual progenitor of soybean, is an excellent example of GP-1 B (Fig. 1). Major economically important legumes are a rich reservoir of GP-1 genetic resources. Breeders are largely confined within GP-1 to broadening the genetic base of legumes (Table 1).

Secondary gene pool

The secondary gene pool (GP-2) includes all the species that can be crossed with GP-1 with some fertility in F_1 s (Fig. 1). Gene transfer is feasible. Faba bean and soybean do not have GP-2. By contrast, common bean and pigeonpea have a large number of species in GP-2, while azuki bean has only 1 species (Table 1).

Tertiary gene pool

The tertiary gene pool (GP-3) is the outer limit of potential genetic resources. Prezygotic and postzygotic barriers can cause partial or complete hybridization failure, thereby inhibiting introgression between GP-1 and GP-3. Exploitation of GP-3 to incorporate traits of economic importance is hampered by poor crossability, early embryo abortion, hybrid inviability, hybrid seedling lethality, and hybrid sterility due to low chromosome pairing. Technology to exploit GP-3 for broadening the genetic base of cultivated legumes is in its infancy. GP-3 species have been identified for major legumes but are unknown for pea and faba bean (Table 1). Pigeonpea, chickpea, and soybean have rich reservoirs of GP-3. Soybean has 26 perennial wild *Glycine* species. They are native to Australia and diverse in morphology, and they

grow in a wide range of agroclimatic conditions. Intersubgeneric F_1 hybrids involving 4 species (*G. argyria*, *G. canescens*, *G. clandestina*, and *G. tomentella*) have been produced and advanced generations of soybean \times *G. tomentella* ($2n = 78$) are also being produced (Singh et al. 2007; R.J. Singh, unpublished data). Forage legumes such as alfalfa, clover, and birdsfoot trefoil have many wild species belonging to GP-3.

Quaternary gene pool

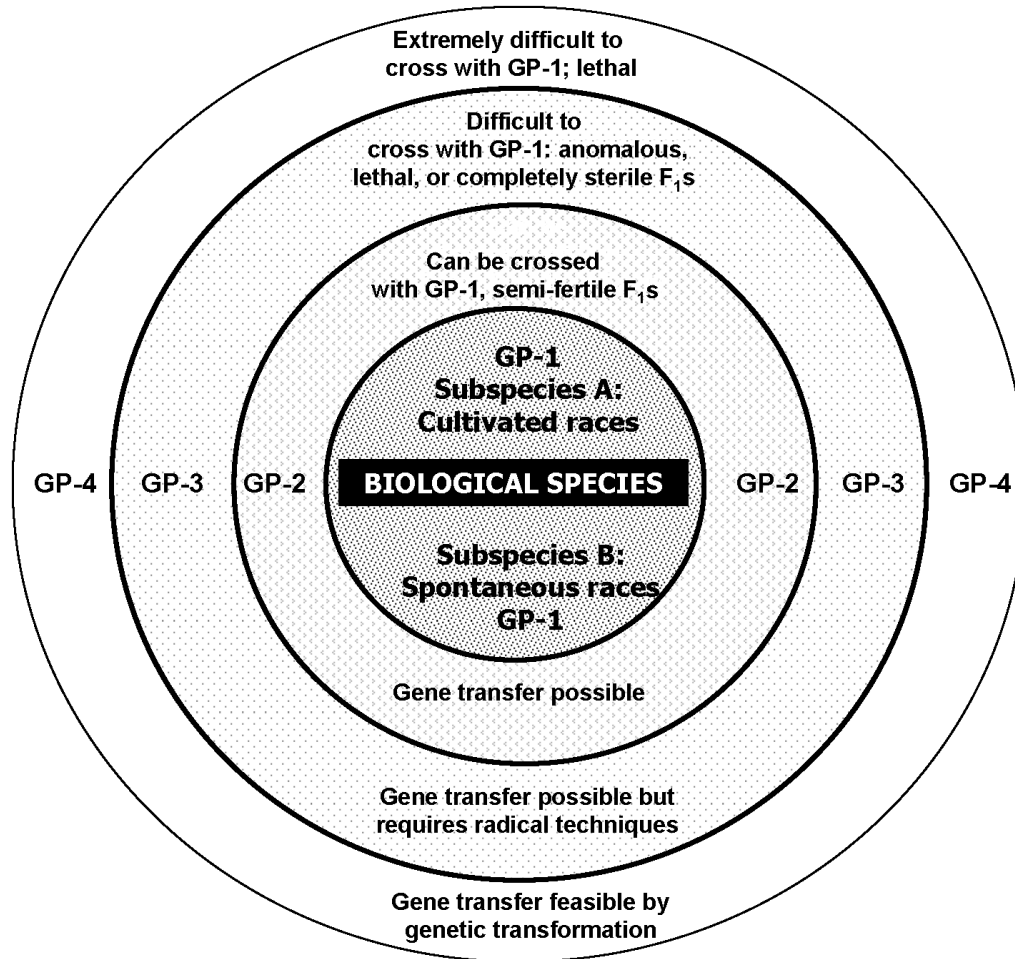
Harlan and de Wet (1971) did not envision a quaternary gene pool (GP-4) based on hybridization experiments when they proposed their gene pool model. Gene cloning and genetic transformation techniques had not been discovered at that time. Wide hybridization in legumes trails that reported for cereals. Pre- and post-hybridization barriers are prevalent within the species of wild relatives of cultigens. For example, not all wild perennial *Glycine* species are cross-compatible. Pod abortion, hybrid seedling lethality, hybrid seed inviability, or complete F_1 seed sterility are common among wild perennial *Glycine* species (Singh et al. 2007). *Phaseolus filiformis* Benth., *P. angustissimus* Gray, and *P. lunatus* L. are considered GP-4 for common bean (Singh 2001). Greene and Morris (2001) included all other non-related and non-cultivated species of the genus *Trifolium* in the quaternary gene pool. Molecular technology has played a pivotal role in establishing phylogenetic relationships in legumes where cytogenetic approaches have failed (Doyle and Luckow 2003). GP-4 designation of economically important legumes is speculative at this time. Introgression of genes from GP-4 to cultigens of legumes may now be feasible by somatic hybridization and genetic transformation technology.

Importance of legumes

Grain legumes (rich in proteins) and cereals (rich in carbohydrates) are an excellent combination for a balanced human diet. Green legumes may be used as a vegetable for humans and as fodder for animals and may be used for soil enrichment through nitrogen fixation or when used as a green manure. Vegetables are the most economical sources of protein for a large proportion of the population in Asia and Africa and are particularly important sources of protein for disadvantaged people. For the world's poor, there is a need for a "protein revolution". Protein energy malnutrition (PEM) affects 1 in 4 children worldwide. Geographically, 70% of children affected by PEM live in Asia, 26% live in Africa, and 4% live in Latin America and the Caribbean (World Hunger Education Service 2006). Consumption of vegetable proteins can reduce PEM for vegetarian populations worldwide (Singh 2007). Legumes are also an excellent source of timber, medicine, tannins, gums, insecticides, fish poisons or molluscicides, resins, varnishes, paints, dyes, and lacquers (International Legume Database and Information Service 2007). Table 2 lists major and minor legumes used for grain, oil, forage, medicine, and industry.

Soybean and related by-products (soymeal, soymilk, and tofu) are a rich source of high-quality protein, essential amino acids, vitamins (vitamin B, including folate), fiber, essential fatty acids (omega-3 fatty acid, alpha linolenic

Fig. 1. Modified gene pool concept in plants, based on hybridization studies (revised from Harlan and de Wet 1971).



acid), phytochemicals, and lecithin. Lecithin is an emulsifier used in pharmaceuticals, cosmetics, paints, plastics, and food (in the manufacture of margarine, bakery goods, and chocolate products) and also in compounds for animal feed (Hatje 1989). Consumption of soybean helps reduce cholesterol and prevent and manage certain types of cancer, kidney disease, osteoporosis, diabetes, and obesity (Illinois Center for Soy Foods 2007). Soymilk and tofu do not contain lactose, saturated fat, or cholesterol. This makes soymilk an excellent substitute for animal milk and milk products, which do contain lactose, saturated fat, and cholesterol and often contain antibiotics. Defatted soy flour, rich in protein and mixed with cereal flour in a ratio of 1:3, is a healthy dietary supplement for vegetarian populations. Food manufacturers add small amounts of soy flour to their baked goods to extend shelf life (National Soybean Research Laboratory 2007). Soybean oil is also used in industrial lubricants and in printing ink. Soybean-oil-based paints, cosmetics, and biodegradable crayons are bio-friendly alternatives. Soy diesel and similar by-products are environmentally friendly replacements for their petroleum-based counterparts (Singh 2007).

Faba bean and velvetbean (*Mucuna pruriens* (L.) DC.) are rich in 3,4-dihydroxyphenylalanine (L-DOPA), which is used to combat the effects of Parkinson's disease and has a po-

tential use in pharmacy. Consumption of common bean reduces cholesterol levels and cancer incidence.

Classification of legumes

Legumes belong to the family Fabaceae, which includes subfamilies Papilionoideae, Mimosoideae, and Caesalpinioideae. Table 3 lists major distinguishing morphological traits among these 3 subfamilies. The unique characteristic of the family is the fruit, a pod, technically known as a legume. The Papilionoideae are easily recognized by their characteristic papilionaceous (butterfly-like) flowers. Soybean has a typical papilionaceous flower, with a tubular calyx of 5 unequal sepals and a 5-part corolla. The corolla consists of a standard (posterior banner petal), 2 lateral wings, and 2 anterior keel petals in contact with each other but not fused (Fig. 2A). Stamens are clustered around the stigma, thus ensuring self-pollination (Fig. 2B). The gynoecium consists of an ovary, style, and stigma (Fig. 2C). As many as 4 ovules appear in the ovary. Nine stamens are arranged in 2 whorls; the outer and inner whorls contain 5 and 4 stamens, respectively (Fig. 2D). The 2 whorls of stamens align themselves in a single whorl on a staminal tube. The larger and older stamens alternate with the smaller and younger stamens in sequence around the developing gynoecium. The single (10th) free stamen is the last to appear (Singh et al. 2007).

Table 1. Common name, scientific name, 2n chromosome number, origin, and gene pools of major legumes.

Common name	Scientific name	2n	Origin	Gene pool			Protein content (%)
				GP-1	GP-2	GP-3	
Common bean	<i>Phaseolus vulgaris</i>	22	Mexico, Middle America, and Andean South America	Domesticated cultigens, wild populations	<i>P. coccineus</i> , <i>P. polyanthus</i> , <i>P. costaricensis</i>	<i>P. acutifolius</i> , <i>P. parvifolius</i>	22 ^a
Pea	<i>Pisum sativum</i>	14	Fertile Crescent, the Mediterranean, and Central Asia	Domestic cultigens, wild relative subspecies, <i>P. pumilio</i> , <i>P. elatius</i> , <i>P. abyssinicum</i>	<i>P. fulvum</i>	None	26 ^a
Pigeonpea	<i>Cajanus cajan</i>	22	India	Cultivated land races	<i>C. acutifolius</i> , <i>C. albicans</i> , <i>C. cajanifolius</i> , <i>C. confertifolius</i> , <i>C. lanceolatus</i> , <i>C. lineatus</i> , <i>C. reticulatus</i> , <i>C. scarabaeoides</i> , <i>C. sericeus</i> , <i>C. trinervius</i>	<i>C. cinereus</i> , <i>C. confertiflorus</i> , <i>C. crassus</i> , <i>C. goensis</i> , <i>C. latisepalus</i> , <i>C. mollis</i> , <i>C. platycarpus</i> , <i>C. rugosus</i> , <i>Dunbaria</i> spp., <i>Rhynchosia</i> spp.	20–22 ^a
Cowpea	<i>Vigna unguiculata</i>	22	Africa	Four cultigroups, land races, and subsp. <i>tenuis</i> , <i>denkindtiana</i> , <i>stenophylla</i>	Subsp. <i>pubescence</i>	<i>V. vexillata</i> , <i>V. radiata</i>	20–26 ^a
Faba bean	<i>Vicia faba</i>	12	Near East	Domestic cultigens	None	None	25–33 ^a
Chickpea	<i>Cicer arietinum</i>	16	Southern Caucasus, northern Persia, and southeastern Turkey	<i>C. arietinum</i> , <i>C. echinospermum</i> , <i>C. reticulatum</i>	<i>C. bijugum</i> , <i>C. judaicum</i> , <i>C. pinnatifidum</i>	<i>C. chorassanicum</i> , <i>C. cuneatum</i> , <i>C. yamashitae</i> , all perennial 34, <i>Cicer</i> spp.	23 ^a
Lentil	<i>Lens culinaris</i>	14	Near East arc and Asia Minor	subsp. <i>culinaris</i> , subsp. <i>odemensis</i> , subsp. <i>orientalis</i>	<i>L. ervoides</i> , <i>L. nigricans</i>	<i>L. lamottei</i> , <i>L. tomentosus</i>	26 ^a
Lupin	<i>Lupinus albus</i>	50	Mediterranean	<i>L. albus</i> var. <i>albus</i> , <i>L. albus</i> var. <i>graeus</i> (wild form)	<i>L. micranthus</i> , ?Western New World <i>Lupinus</i> spp.	All other Old and New World <i>Lupinus</i> spp.	36.1 ^a
	<i>Lupinus luteus</i>	52	Mediterranean	Wild forms, land races, cultivars, subsp. <i>orientalis</i>	<i>L. hispanicus</i> subsp. <i>bicolor</i> , subsp. <i>hispanicus</i>	All other Old and New World <i>Lupinus</i> spp.	38.3 ^a
	<i>Lupinus angustifolius</i>	40	Mediterranean	All wild, land race, and domesticated forms of <i>L. angustifolius</i>	<i>L. luteus</i> , <i>L. hispanicus</i>	All other Old and New World <i>Lupinus</i> spp.	32.2 ^a
	<i>Lupinus cosentinii</i>	32	Mediterranean	<i>L. digitatus</i> , <i>L. atlanticus</i> , <i>L. pilosus</i>	<i>L. palaestinus</i> , <i>L. princei</i> , <i>L. somaliensis</i>	All other Old and New World <i>Lupinus</i> spp.	32.1 ^a
	<i>Lupinus mutabilis</i>	48	South America	?Western North and South American species with 2n = 48	<i>L. albus</i> , <i>L. micranthus</i>	All other Old World and western New World <i>Lupinus</i> spp.	44 ^a
Mungbean	<i>Vigna radiata</i>	22	India	<i>V. radiata</i> var. <i>radiata</i> , <i>V. radiata</i> var. <i>sublobata</i>	<i>V. mungo</i> , <i>V. subramaniana</i> , <i>V. stipulacea</i>	Sect. <i>Aconitifoliae</i> , Sect. <i>Angulares</i> , <i>V. grandiflora</i>	22.9 ^a
Azuki bean	<i>Vigna angularis</i>	22	East Asia	<i>V. angularis</i> var. <i>angularis</i> , <i>V. angularis</i> var. <i>nipponensis</i> , <i>V. hirtella</i> , <i>V. minima</i> , <i>V. nakashimae</i> , <i>V. nepalensis</i> , <i>V. riukiensis</i> , <i>V. tenuicaulis</i>	<i>V. umbellata</i>	Sect. <i>Ceratotropis</i> , <i>V. trinervia</i>	21.1 ^a
Soybean	<i>Glycine max</i>	40	East Asia – China	<i>G. soja</i>	None	Subgenus <i>Glycine</i>	40 ^b
Groundnut	<i>Arachis hypogaea</i>	40	South America	<i>A. hypogaea</i> , <i>A. monticola</i>	Sect. <i>Arachis</i>	Sect. <i>Rhizomatosae</i> , Sect. <i>Erectoides</i> , Sect. <i>Extranervosae</i> , Sect. <i>Ambinervosae</i> , Sect. <i>Triseminalae</i>	25 ^b
Guar	<i>Cyamopsis tetragonoloba</i>	14	India, Pakistan	Cultivars, land races, <i>C. tetragonoloba</i>	<i>C. dentate</i> , <i>C. senegalensis</i> , <i>C. serrata</i>		23–31 ^c

^aSingh 2005.^bSingh 2007.^cKays et al. 2006.

Table 2. Economically important valuable traits in legumes.

Common name	Botanical name	Use
Alfalfa	<i>Medicago sativa</i> L.	Forage (one of the species, <i>Medicago truncatula</i> , is a model crop for genomic studies)
Azuki bean	<i>Vigna angularis</i> (Willd.) Ohwi & Ohashi	Confectionary (21% protein, rich in complex carbohydrates, minerals, and vitamins)
Birdsfoot trefoil	<i>Lotus corniculatus</i> L.	Forage (one of the species, <i>Lotus japonicus</i> , is a model crop for genomic studies)
Butterfly pea	<i>Clitoria ternatea</i> (L.)	Forage, cover crop, ornamental (medicinal value: antifungal protein)
Chickpea	<i>Cicer arietinum</i> L.	Pulse (23% protein, rich in minerals and amino acids)
Common bean	<i>Phaseolus vulgaris</i> L.	Pulse, vegetable (22% protein, rich in amino acids, minerals, and vitamins, reduces cholesterol and cancer)
Cowitch	<i>Mucuna pruriens</i> (L.) DC.	Pulse (medicinal value: treating abdominal pain, cholera, diabetes, infertility, Parkinson's disease, scorpion bites, snakebites, and toothache)
Cowpea	<i>Vigna unguiculata</i> (L.) Walp.	Pulse, vegetable (20%–26% protein, rich source of calcium, iron, and zinc)
Dhaincha	<i>Sesbania bispinosa</i> (Jacq.) W. Wight	Fodder, fiber, green manure, cover crop, pulp, paper, gum
Faba bean	<i>Vicia faba</i> L.	Pulse, vegetable (25%–33% protein, rich in 3,4-dihydroxyphenylalanine (L-DOPA, used against Parkinson's disease))
Fennugreek	<i>Trigonella foenum-graecum</i> L.	Spice, vegetable (31% protein, rich in minerals and vitamin A, lowers blood sugar in diabetics)
Grass pea	<i>Lathyrus sativus</i> L.	Pulse, fodder (rich in protein, contains neurotoxin (b-ODAP) causing neurolathyrism)
Groundnut	<i>Arachis hypogaea</i> L.	Food (confectionary), oil (25% protein, 50% oil, rich in high-quality protein with essential amino acids and fatty acids, vitamins, and phytochemicals; industrial use)
Guar	<i>Cyamopsis tetragonoloba</i> (L.) Taub.	Vegetable, forage, gum, green manure (35% protein, industrial use: stiffener in soft ice cream, a stabilizer for cheese, instant puddings, and whipped cream substitutes, and a meat binder; cholesterol reduction)
Hyacinth bean	<i>Lablab purpureus</i> (L.) Sweet	Forage, pulse, ornamental (medicinal value: antihypertensive)
Indigo	<i>Indigofera arrecta</i> Hochst. ex A. Rich	Dye
Jackbean	<i>Canavalia ensiformis</i> (L.) DC.	Pulse, forage, green manure (medicinal value: anticancer, antitumor, and anti-viral)
Jumbie bean	<i>Leucaena leucocephala</i> (Lam.) de Wit	Forage, fiber, fuel, green manure, food, timber, soil conservation
Kudzu	<i>Pueraria montana</i> var. <i>lobata</i> (Willd.) Maesen & S. Almeida	Forage, food (medicinal value: anti-inflammatory, antimicrobial, coronary dilator, estrogenic, cancer preventive, antileukemic, hypoglycemic)
Lentil	<i>Lens culinaris</i> Medik.	Pulse (26% protein, rich in vitamins, minerals, fiber, amino acids)
Lupin	<i>Lupinus</i> species	Feed, forage (36%–44% protein)
Mungbean	<i>Vigna radiata</i> (L.) Wilczek	Pulse, vegetable (22.9% protein, rich in minerals, amino acids, and vitamins)
Pea	<i>Pisum sativum</i> L.	Pulse, vegetable (26% protein, rich in minerals, vitamins, and amino acids)
Pigeonpea	<i>Cajanus cajan</i> (L.) Millsp.	Pulse, vegetable, fuel (20%–22% protein, rich in vitamins, fiber, minerals, and carbohydrates)
Red clover	<i>Trifolium pratense</i> L.	Forage (a model crop for genomic studies; prevents osteoporosis)
Soybean	<i>Glycine max</i> (L.) Merr.	Feed, food, oil (40% protein, 20% oil, rich in high-quality protein with essential amino acids and fatty acids, vitamins, fiber, phytochemicals, and lecithin; industrial lubricants, soy diesel, and printing ink; cholesterol reduction)
Sunn hemp	<i>Crotalaria juncea</i> L.	Fiber, green manure (medicinal value: antitumor, anti-diarrhea)
Wingbean	<i>Phosphocarpus tetragonolobus</i> (L.) DC.	Vegetable (34%–37% protein, medicinal value: antitumor)

Note: Sources: Morris 1999, 2004; Small 1999; Singh 2005, 2007.

Cytogenetics of legumes

Classical cytogenetics of legumes

Cytogenetic research of legumes has not progressed as rapidly as that for cereals, and cytogenetic knowledge of major grain legumes, oilseed crops, and forage crops is lack-

ing. The only exception is faba bean. Taylor et al. (1957) demonstrated semiconservative replication of faba bean chromosomes by using tritium-labeled thymidine. Faba bean has been used as a model crop to teach students cytology and to study the effect of chemicals on chromosome structure because it contains only a few large chromosomes ($2n = 12$).

Table 3. Main distinguishing morphological traits of three legume subfamilies (from Lewis et al. 2005, reproduced with permission of Royal Botanic Gardens, Kew, © 2005).

Caesalpinioideae	Mimosoideae	Papilionoideae
Tree, shrubs, lianas	Tree, shrubs, lianas, rarely aquatic plants	Herbs, shrubs, trees, lianas, twiners
Flowers relatively large	Small regular flowers aggregated into heads	Pea flowers
Flowers generally zygomorphic	Flowers actinomorphic, radially symmetrical	Flowers zygomorphic
Petals imbricate in bud	Petals valvate in bud	Petals imbricate in bud
Median petal overlapped by others (when present)	Median petal not overlapped by others, similar in shape and size	Median petal (standard, banner, or vexillum) overlaps others (these occasionally absent)
Sepals generally free	Sepals generally united at the base	Sepals united at base into a calyx tube
Seeds generally without pleurogram (if present, closed); also without a hilar groove	Seeds usually with open pleurogram	Seeds (if hard) with complex hilar valve (bean and peas); pleurogram absent
Embryo radicle usually straight	Embryo radicle usually straight	Embryo radicle usually curved
Leaves bipinnate or pinnate (rarely simple or 1-foliate)	Leaves mainly bipinnate and often with specialized glands; Australian acacias have phyllodes	Leaves 1-foliate to once pinnate (a few palmate); some with tendrils; only one rare species bipinnate
Stamens (1-) 10 (-many); sometimes dimorphic or heteromorphic	Stamens (3-) 10-many (sometimes over 100); all the same	Stamens (9-) 10-many (sometimes dimorphic)
Petals most showy part	Stamens most showy part	Petals most showy part
Compound pollen (polyads) rare	Compound pollen (polyads) common	Pollen in single grains
Root nodules uncommon, but many associations with fungi	Root nodules generally present	Root nodules generally present

Classical genetic linkage maps (CGLMs) for major legumes have been developed by using morphological markers. Most of the linkage maps contain 2 loosely associated markers. In legumes, association of CGLMs to specific chromosomes by using aneuploid stocks has lagged behind such research in rice, maize, barley, and tomato. Five of the possible 6 primary trisomics have been isolated in faba bean and linkage groups have been assigned to specific chromosomes (Román et al. 2004). Although Mendel's law of inheritance was established with pea experiments in 1865 and was rediscovered in 1900, a consensus linkage map of pea was not developed until 1998 (Weeden et al. 1998). Neumann et al. (2001) isolated 32 clones in pea ranging from 149 to 2961 bp and conducted a comparative study of the distribution of repetitive pea sequences in 20 legumes, including *Arabidopsis thaliana*, using fluorescence in situ hybridization (FISH). The tandem repeats were mostly specific to the genus *Pisum* and many of the dispersed repeats were detected in species of the genus *Vicia* but were absent in *C. arietinum* and *A. thaliana*.

Although the precise chromosome number of soybean, an economically important oilseed crop, was determined in 1925 (Karpechenko 1925), the chromosome map was not developed based on somatic metaphase chromosomes because the chromosomes are symmetrical and only a pair of nucleolus organizer chromosomes are easily identified (Fig. 3). Singh and Hymowitz (1988) constructed a soybean chromosome map by using pachytene chromosomes. The length of chromosome 1 was 39.79 μm and that of chromosome 20 was 10.63 μm , and 35.8% of the soybean genome was found to be heterochromatic. Furthermore, the short arms of 6 of the 20 bivalents (chromosomes 5, 7, 10, and 18–20) were completely heterochromatic. In contrast, the range of somatic chromosome length was 1.42 μm to

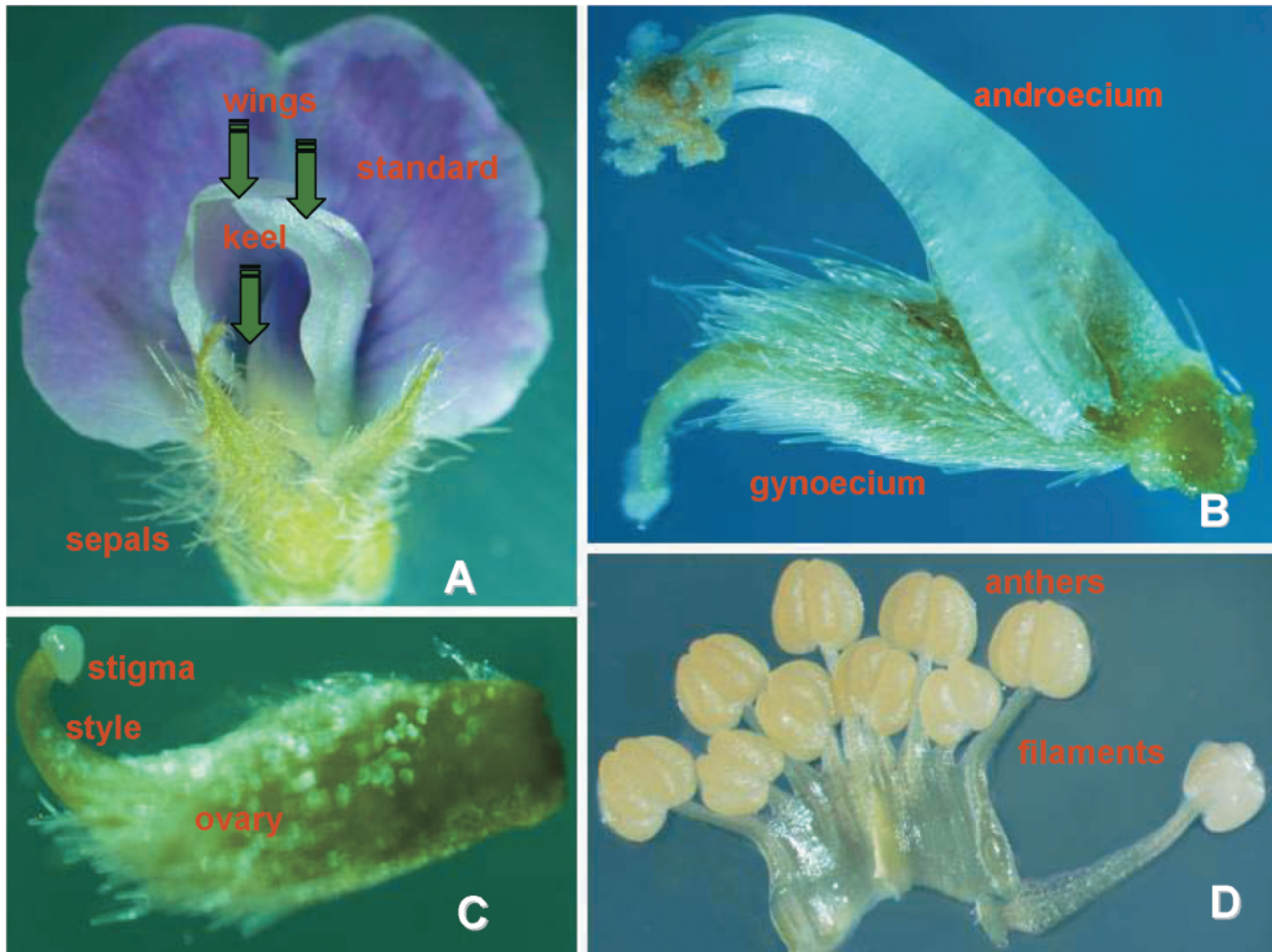
2.84 μm (Sen and Vidyabhusan 1960). This pioneering research has set the stage to develop and use primary trisomics to associate the CGLM and the molecular genetic linkage map of soybean with specific chromosomes (Xu et al. 2000; Zou et al. 2003). However, seeds of primary trisomics and tetrasomics are not available (Singh et al. 2007). The possible CGLMs of soybean have been proposed (Palmer et al. 2004).

Molecular cytogenetics of legumes

Studies on developing molecular linkage maps for several legumes have progressed rapidly, particularly in 3 forage legumes (*L. japonicus*, *M. truncatula*, *T. pratense*) that are considered model crops for genome sequencing. In major grain legumes (pea, faba bean), oilseed crops (soybean), and forage crops (particularly *M. truncatula*, *T. pratense*, and *L. japonicus*), a composite molecular linkage map has been successfully developed using isozymes, seed protein genes, random amplified polymorphic DNAs (RAPDs), restriction fragment length polymorphisms (RFLPs), sequence-characterized amplified regions (SCARs), amplified fragment length polymorphisms (AFLPs), and simple sequence repeats (SSRs) or microsatellites.

Molecular linkage groups in soybean have been developed by several laboratories using various molecular markers (Song et al. 2004), but the association of CGLM to cytologically identifiable chromosomes is unknown. Molecular cytogenetic mapping has progressed at a very rapid pace in the model forage crops *M. truncatula* (Kulikova et al. 2001, 2004), *T. pratense* (Sato et al. 2005), and *L. japonicus* (Sandal et al. 2002; Pedrosa et al. 2002). Kulikova et al. (2001) developed a molecular cytogenetic map of *M. truncatula* ($2n = 2x = 16$) on the basis of a pachytene FISH karyotype. Like soybean chromosomes, *M. truncatula*

Fig. 2. Reproductive organs of soybean: (A) complete mature flower; (B) mature androecium and gynoecium; (C) mature gynoecium with stigma, style, and ovary; (D) mature anthers with 5 anthers on longer filament (outer whorl), 4 anthers on shorter filament (inner whorl), and 1 free anther always below the stigma (from Singh et al. 2007, reproduced by permission of CRC Press, a division of Taylor & Francis Group, © 2007).



pachytene chromosomes are 20 times longer than the mitotic metaphase chromosomes. Sato et al. (2005) investigated the genome structure of *T. pratense* using cytological, genomic, and genetic approaches. They used 1472 informative markers (1305 microsatellite and 167 RFLP markers) and assigned 1463 loci to 7 linkage groups. Each linkage group was associated with individual chromosomes by FISH analysis. Sandal et al. (2002) constructed 6 linkage groups of *L. japonicus* by using 524 AFLP markers, 3 RAPD markers, 39 gene-specific markers, 33 SSR markers, and 6 recessive symbiotic mutant loci. Linkage groups were again associated with the respective chromosomes by FISH analysis (Pedrosa et al. 2002).

Molecular cytogenetic maps are constructed from F_2 populations derived from interspecific hybrids. Molecular marker segregation distortion in *T. pratense* ranged from 7.7% (linkage group 5) to 52.3% (linkage group 2) (Sato et al. 2005). Segregation distortion along the length of the chromosomes and to specific chromosomes of *L. japonicus* was attributed to paracentric and pericentric inversions, deletions, and translocations. The clustering of markers on the linkage map positions corresponding to the top of the short

arm of chromosome 2 and part of chromosome 4 was attributed to the suppression of recombination in these regions (Sandal et al. 2002; Pedrosa et al. 2002). Heterochromatin also influences recombination by distorting segregation. While studying primary trisomics, Zou et al. (2006) reported segregation distortion for 4 SSR markers examined with chromosomes 4, 13, and 17 of soybean; these chromosomes are highly heterochromatic (Singh and Hymowitz 1988).

Phylogenetic studies in legumes

A clear understanding of legume phylogeny is credited to many laboratories using plant exploration, preservation, morphological characterization, chromosome counting, and comprehensive molecular methods. Readers are advised to consult papers by Doyle and Luckow (2003), Wojciechowski et al. (2004), and Lavin et al. (2005) and an exhaustive monograph by Lewis et al. (2005). Lewis et al. (2005) constructed a super phylogenetic tree of the Leguminosae based on published molecular data. The subfamily Caesalpinioideae comprises 4 tribes (Cercideae, Detarieae, Cassieae, and Caesalpinieae). The subfamily Mimosoideae is composed of the tribes Mimosoideae, Mimoseae, Acacieae, and In-

Fig. 3. A mitotic metaphase cell of soybean with $2n = 40$ chromosomes. One pair of chromosomes containing a nucleolus organizer region (NOR) can be distinguished, while 38 chromosomes are almost similar (from Singh et al. 2007, reproduced by permission of CRC Press, a division of Taylor & Francis Group, © 2007).



geae. The subfamily Papilionoideae consists of crops of the cool- and warm-weather groups. It has 28 tribes originating from several main groups. These groups are Swartzieae *sensu stricto*, the Genistoid clade, the Andira group, the Amorphaeae, the Dalbergoid clade, and the Old World clade.

Genomic studies in legumes

Three forage legumes, namely *L. japonicus*, *M. truncatula*, and *T. pratense*, are considered model legumes for genomic studies and genome sequencing (Gepts et al. 2005; Choi et al. 2004; Sato et al. 2005; Young et al. 2005; Cannon et al. 2006). These model forage legumes contain genomes about $10\times$ smaller than the genome of *P. sativum*. Although soybean is an ancient diploidized allotetraploid ($2n = 40$) (Singh et al. 2007), it is a candidate for genomic studies and genome sequencing because of its economic importance. It has a genome about $5\times$ smaller than that of pea (Table 4). Currently in the United States, the Joint Genome Institute of the US Department of Energy is sequencing the soybean genome, and a genome initiative has been established in collaboration with the USDA-ARS and the National Science Foundation. Significant soybean sequencing initiatives are also underway in China, Japan, and South Korea, and international coordination is being planned. The completed sequence of the soybean genome will be a major advance for legume genetics.

Germplasm resources of legumes

All international and national institutes for grain legumes, oilseed crops, forage legumes, and other economically important shrub and tree legumes collect, maintain, disseminate, and develop breeding lines with resistance to abiotic and biotic stresses. Plant germplasm exploration for wild relatives of common bean, faba bean, lentil, chickpea, and cowpea is extensive. Although pea is an important legume, no international institute has a mandate for this crop, but several research institutes maintain active programs. The National Institute of Agrobiological Sciences in Japan has a very active research program for the Asian species of *Vigna*,

including mungbean and azuki bean (Tomooka et al. 2002; Maxted et al. 2004; Freytag and Debouck 2002). The legume collections at Kew Gardens (London, UK) comprise approximately 725 000 specimens and are among the most comprehensive in the world (Lewis et al. 2005).

Some high-yielding cultivars are eroding the natural habitat of allied species and genera. These invaluable germplasm resources should be collected before they become extinct. International and national institutes are preserving indigenous varieties, land races, wild progenitors, and wild relatives in medium- and long-term storage. Varietal improvement programs develop elite breeding lines. Development of improved lines of economic importance is dependant upon the breeding objectives, the type of legume (cross- vs. self-pollinated, long- vs. short-term reproductive cycle), end-use products (pulses, meals, oils, and by-products), breeding methods (conventional vs. molecular-aided breeding), and the costs and benefits of raising a particular crop (supply and demand, market value). Other important criteria include inheritance patterns and heritability of the selected characters, such as anti-nutritional factors. Other breeding objectives are improved quantity and quality of proteins and fatty acids free from food allergens, yield heterosis, plant architecture modification, earliness, stress resistance, and resistance to shattering and lodging. Breeding lines may be improved from available germplasms, mutation breeding, and genetic transformation.

Core collection

The concept of a core collection was developed in the 1980s (Frankel and Brown 1984) to make germplasm collections, which continue to increase in size, more accessible to potential users. Core collections usually contain only 10% of accessions of the total core collection, but depending on the size and diversity of the collection, that number may vary from 5% to 20%. A well-selected core collection can contain 70% or more of the alleles that exist in the total collection (Brown 1989). Core collections are generally established using a stratified sampling procedure. Accessions are divided into non-overlapping groups that may be based on species, origin, plant type, or available morphological or genetic data. A variety of selection strategies and data can be used to select accessions from each group to form the final core collection. Core collections exist for many legume collections and those for pigeonpea (Reddy et al. 2005), groundnut (Holbrook et al. 1993), and annual (Diwan et al. 1995) and perennial *Medicago* species (Basigalup et al. 1995) are illustrative of the various stratified sampling procedures. Some core collections may still be too large for some applications, so subsets of core collections called mini cores have been developed for some collections (Holbrook and Dong 2005).

For example, the entire ICRISAT groundnut collection (14 310 accessions) was reduced to a core collection of 1 704 accessions. Further evaluation reduced the core collection to 184 accessions known as the mini core (core of core). The mini core of 184 accessions represents most of the genetic diversity of the entire ICRISAT collection. It has been suggested that the mini core collection may be used to improve the efficiency of identifying desirable traits

Table 4. Genome size of eight legumes.

Botanical name	Common name	<i>n</i>	Genome size (Mb)	Tribe
<i>Trifolium pratense</i>	Red clover	7	440 ^a	Trifoleae
<i>Medicago truncatula</i>	Barrel medic	8	500 ^b	Trifoleae
<i>Lotus japonicus</i>	Birdsfoot trefoil	6	500 ^b	Loteae
<i>Vigna radiata</i>	Mungbean	11	520 ^b	Phaseoleae
<i>Phaseolus vulgaris</i>	Common bean	11	620 ^b	Phaseoleae
<i>Glycine max</i>	Soybean	20	1100 ^b	Phaseoleae
<i>Medicago sativa</i>	Alfalfa	16	1600 ^b	Trifoleae
<i>Pisum sativum</i>	Pea	7	5000 ^b	Viceae

Note: *n*, gametic chromosome number.

^aSato et al. 2005.

^bChoi et al. 2004.

in the core collection and in the entire collection (Liao and Holbrook 2007).

Breeding for high-yielding legumes

The present genetic base of grain legumes including oil-seed crops (soybean and groundnut) is extremely narrow because breeders have largely confined their varietal improvement programs to GP-1. However, substantial gain in yield has been achieved in major pulses and oilseed legumes through innovative conventional breeding, although it is far behind that of cereals. Production of high-yielding wheat and rice, and the ensuing green revolution, was achieved by using dwarfing genes that allowed the production of varieties that were more responsive to additional inputs such as fertilizer.

In the US, a maturity group classification for soybean was initially established in 1941 to distinguish among soybean varieties. The USDA organized regional yield tests of experimental lines of differing maturities (groups I, II, and III). The system continued to expand to cover all soybean growing regions of the US and the range of diversity represented in the USDA Soybean Germplasm collection. The final maturity group (000) was added around 1970 to accommodate the very earliest maturing accessions, so the current system includes 13 groups from 000 to X. This system is also used in other countries but it is not well suited for regions with complex cropping systems (Wang et al. 2006).

Mutation breeding has produced soybean cultivars with high yield in China, Japan, and Korea (Singh and Hymowitz 1999). Groundnut breeders in China used only 2 local varieties, Fahuasheng and Shitouqui, in varietal improvement. Their pedigree could be traced in more than 60% of the groundnut cultivars released. Most of the groundnut varieties released are from conventional breeding methods (Liao and Holbrook 2007).

Through conventional breeding approaches, breeders have developed determinate semi-dwarf and dwarf plant ideotypes with uniform maturity for pea, cowpea, faba bean, common bean, pigeonpea, lupin, mungbean, azuki bean, and soybean. Semi-dwarf varieties (determinate plant type) are resistant to lodging and are adapted to mechanical harvesting. Early maturing (<98 days), high-yielding common bean varieties with an upright growth habit can be harvested by machine. This is cost-effective for common bean growers. Dwarfing genes in pigeonpea have been identified and are being used to de-

velop dwarf pigeonpea. Most pigeonpea varieties at the reproductive stage achieve heights of 2–3 m. The dwarf-inbred lines range in height between 70 and 80 cm and produce reasonable yields (see Singh 2005, 2007).

Anti-nutritional elements in legumes

Grain legumes are a rich source of protein (Table 1). They are used for animal feed and for human consumption in forms such as *dhal* or soup. Protein content in pigeonpea ranges from 20% to 22%. Its wild relatives have protein contents of up to 32% and lines with high protein content have been developed from these materials (Singh 2005). The nutritional value and industrial suitability of oil seed crops are determined by their fatty acid composition.

Legumes also contain numerous anti-nutritional elements that reduce their biological value and are undesirable for humans and animals when legumes are consumed raw. For example, faba bean contains tannins, vicine, convicine, and 2 glycosides related to favism. Favism causes strong stomach hemorrhaging. Cowpea and pigeonpea contain trypsin and chymotrypsin inhibitors and tannins. A large fraction (50% of total) of seed protein in common bean constitutes the storage protein phaseollin. Phytohemagglutinin and lectin-related proteins in bean seeds are toxic to monogastric animals. Groundnut contains an aflatoxin that causes severe allergic reaction in a certain group of individuals. This sometimes leads to death if immediate medical treatment is not administered.

Mechanical processing and breeding methods have reduced the anti-nutritional elements in faba bean. The development of lupins as a modern crop plant began with the selection of plants with reduced alkaloid content in seeds. However, these elements can be eliminated by heat treatment and by varietal improvement. Cowpea is a rich source of calcium, iron, and zinc, which are desirable from a nutritional perspective. These elements may increase seed hardness and cooking time. Soaking of seeds before cooking reduces cooking time. Common bean without phytohemagglutinin has been produced by conventional backcrossing methods (Singh 2005).

Wild relatives of cultigens often do not contain anti-nutritional factors. These traits could be introgressed into cultigens once wide hybridization techniques are developed. Soybean seed protein contains an undesirable Kunitz trypsin inhibitor, which may be removed by treating

the moist seed with heat or genetically eliminated (Bernard et al. 1991). Groundnut cultivars resistant to aflatoxin contamination are being developed. Transformation may also play a key role in producing grain legumes without anti-nutritional elements. Several laboratories worldwide are engaged in producing transgenic legumes (Singh 2005, 2007).

Hybrid legumes—a dream

Commercial hybrids using cytoplasmic male sterility (CMS) systems have been developed for pigeonpea. Hybrid seeds developed in conjunction with CMS lines yield 4% to 52% more than the parents. This is feasible because the natural out-crossing in pigeonpea ranges from 20% to 40%. However, the major obstacle to producing hybrid legumes is flower morphology, which ensures 99% self-pollination in many species except faba bean and pigeonpea (Saxena 2005). Lentil contains small cleistogamous flowers, which are virtually 100% self-pollinating. Outcrossing in mungbean is 0.5%–3% (see Singh 2005).

Attempts to produce commercial hybrid soybean cultivars have not succeeded because (i) a good system of producing male sterile plants is not available; (ii) soybean pollen must be carried by insect vectors (soybean flowers are generally unattractive to insects, so even on male-sterile plants, seed set is often low); and (iii) the difficulty in producing hybrids greatly limits the parental combinations that can be tested to find commercially acceptable heterosis. A patent has been granted for hybrid soybean production (Davis 1985). The methodology remains on the books, but its application in hybrid soybean production has not been realized.

Somaclonal variation and genetic transformation in legumes

A somaclonal variant in pigeonpea that produces white seeds exhibits a 25% increase in seed size and a 30% increase in yield (Saxena 2005). Transformation techniques have been developed in several national and international laboratories to incorporate genes for resistance to pests and pathogens in grain legumes. A stable glyphosate-tolerant soybean known as Roundup Ready® soybean has been produced by genetic transformation (see Singh et al. 2007).

Breeding for canning quality

Major advances in breeding of some grain legumes (common bean, faba bean, cowpea, and chickpea) have been made for producing varieties with improved canning characteristics. This has revolutionized the breeding programs for the canning industries. For example, major market classes of common bean developed for canning include Bayo, Great Northern, ‘Ojo de Cabra’ (creamed-striped), pinto, pink, and red Mexican beans. The dark red kidney bean cultivar ‘Montcalm’, which has excellent canning quality, was developed by conventional breeding techniques. Green seeds are canned for local consumption and exported in Puerto Rico and the Dominican Republic (see Singh 2005).

Breeding for vegetable type

Vegetable types of grain legumes command high market prices, particularly common bean, pea, cowpea, pigeonpea, faba bean, chickpea, guar, and lablab. Snap bean cultivars with green pods are known as French, garden, green, or stringless beans. Snap beans with flat or cylindrical pods, yellow (waxy type), green, or purple colors, and long or short pods are all used for fresh, frozen, and canning purposes. Cowpeas with edible pods are widely grown in various Asian and Pacific countries. IITA has developed vegetable-type cowpea varieties, and ICRISAT has released several vegetable-type pigeonpea varieties. One such pigeonpea variety (ICPL 87079) is popular in India, Africa, and China. Green pigeonpea is an important vegetable in the Caribbean. Immature-type peas are used to produce canned or quick-frozen products. The AVRDC breeds an edible vegetable soybean known as *edamame* (fresh green soybean), which is now available in Oriental grocery stores and health food stores. ADF Food Limited produces canned guar vegetables known as Papdi, while House of Spices (India) produces dry lablab vegetable seed. Both guar and lablab are available in Indian grocery stores in the Atlanta, Georgia, area (Brad Morris, personal communication, 27 March 2007).

Conclusion

Legumes are members of the family Fabaceae or Leguminosae, are the third largest flowering plants, and include approximately 727 genera and 19 325 species. They grow in diverse agro-geo-climatic conditions and range from herbs to giant trees. Legumes are economically important in the world trade because they are used for human food, animal feed, and other commercial applications. Vegetable proteins are the most economical source of protein for a large proportion of the population in impoverished countries. These countries need to accomplish a “protein revolution” by increasing the yield of major legumes. Legumes and cereals have been an integral part of human civilization. Legumes (rich in proteins) and cereals (rich in carbohydrates) are an excellent combination for a balanced human diet. Crop rotation of legumes with cereals enriches the soil because legumes fix nitrogen in soil in symbiotic association with nitrogen-fixing bacteria. Legumes contain heart-healthy nutrients and antioxidants. Moderate consumption of such legumes helps to prevent cardiovascular disease, stroke, Parkinson’s, Alzheimer’s, and Huntington’s diseases, liver ailments, and even cancer. Genome sequencing of *M. truncatula*, *L. japonicus*, *T. pratense*, and *G. max* is a milestone of international collaboration using a combination of cytological, genetic, and molecular technologies.

Acknowledgments

We thank Daniel Debouck, Govindjee, Bill Grant, Brad Morris, Joseph Nicholas, Duncan Vaughan, and David Walker for review of the manuscript.

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